

Phylogenetic Properties of *Ohomopterus iwawakianus*
(Coleoptera, Carabidae) as Evidenced by the Sequence Comparisons
of Mitochondrial ND5 Gene and Nuclear Internal Transcribed
Spacer I: Extensive Participation of *O. iwawakianus* in the
Faunal Establishment of the Genus *Ohomopterus*
in the Kinki District

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Abstract Phylogenetic trees of the ND5 gene and nuclear internal transcribed spacer I (ITS I) of *Ohomopterus iwawakianus* and its related taxa have been constructed. The trees strongly suggest that the population represented by subsp. *kiensis* should be regarded as an authentic species and the nominotypical *iwawakianus* and two other subspecies are considered to be offspring of the hybrid between *kiensis* and *O. maiyasanus*. *Ohomopterus iwawakianus* would have played an important role in the faunal formation of the genus *Ohomopterus* in the Kinki District.

Introduction

Ohomopterus iwawakianus is a medium-sized carabid beetle endemic to west-central Honshu in Central Japan. It was originally described by NAKANE (1953) as a subspecies of *Apotomopterus yaconinus* (= *Ohomopterus yaconinus* in the present sense). Ten years later, KAMIYOSHI (1963) raised its rank to a full species based on the morphological studies of the female genitalia. Since the copulatory piece of the male genital organ of NAKANE's race is different in the shape from that of *O. yaconinus*, its status as a distinct species has been kept unchanged by most authors (HIURA, 1965; KATSURA *et al.*, 1978; Kinki Research Group of Carabid Beetles, 1979; ISHIKAWA, 1985; ISHIKAWA & KUBOTA, 1996; IMURA & MIZUSAWA, 1996, etc.). Another lower taxon, named *kiensis*, was also described as a subspecies of *A. yaconinus* by NAKANE and IGA in the same paper as that of *iwawakianus*. It was once raised to a full species

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by KAMIYOSHI (1963), but soon downgraded to a subspecies of *iwawakianus* by HIURA (1965). Since the copulatory piece of *kiiensis* is very similar in the shape to that of *iwawakianus*, HIURA's view has been adopted thereafter by most authors (KATSURA *et al.*, 1978; Kinki Research Group of Carabid Beetles, 1979; ISHIKAWA, 1985; IMURA & MIZUSAWA, 1996, etc.). In 1996, ISHIKAWA and KUBOTA made a tentative revision of *O. iwawakianus* (= *Carabus (Ohomopterus) iwawakianus* in their sense) and classified it into five subspecies, namely, nominotypical *iwawakianus*, *kiiensis*, *narukawai*, *shima* and *muro*. Of these, the latter three were described at that time. Thus, the taxon *iwawakianus* is now generally regarded as an independent polytypical species. Though the adopted genus has been different according to the authors, we use *Ohomopterus* after IMURA (2002) and OSAWA *et al.* (2004).

Ohomopterus iwawakianus as defined above is distributed in the central and southern parts of the Kinki District. The southernmost and greater part of its distributional range is occupied by subsp. *kiiensis*. Each of four other subspecies has much more restricted range and is rather sporadically distributed in the areas adjoining the northeastern periphery of the range of subsp. *kiiensis*. For the detailed distributional map, see Kinki Research Group of Carabid Beetles (1979, p. 27) and ISHIKAWA and KUBOTA (1996, p. 40).

In the present paper, we have constructed the phylogenetic trees of the mitochondrial ND5 gene and nuclear internal transcribed spacer I (ITS I) of *O. iwawakianus* together with the related species mainly from the Kinki District. The results suggest that the population represented by subsp. *kiiensis* should be regarded as an independent species, whereas the other races of *O. iwawakianus* including the nominotypical one are considered to be hybrid-descendants between *kiiensis* and most probably *O. maiyasanus*. The expansion of the distributional range of *O. iwawakianus* has played an indispensable role to form the quite complicated *Ohomopterus* fauna in the Kinki District through its hybridization with several other species.

The last author, Syozo OSAWA (S. O.), wishes to dedicate this paper to the late Dr. Michio CHÛJÔ, who was one of the most distinguished and respectable entomologists, and encouraged S.O. for more than 55 years until he regrettably passed away at the age of 95.

Materials and Methods

The specimens analyzed in this study were shown in the phylogenetic trees (Figs. 1 & 2). DNA sequencing of the ND5 gene and ITS I, and construction of the phylogenetic trees were performed as already described (SU *et al.*, 1996; TOMINAGA *et al.*, 2005). The accession numbers for DDBJ, EMBL and GenBank of the specimens used in this study will be given in the compilatory paper on the molecular phylogenetic studies of the Japanese *Ohomopterus* to be published in the near future.

Results

The scientific names used herein are the same as those currently adopted by the taxonomists, which are based on the morphological classification without considering any molecular data. In this section, those especially relevant to the discussion were indicated by the bold faced letters.

Phylogenetic tree of the ND5 gene (Fig. 1)

Four clusters (I to IV) were recognized in the ND5 phylogenetic tree (Fig. 1 a).

The cluster I (*arrowianus*-lineage; see TOMINAGA *et al.*, 2005, fig. 1) was composed mainly of *O. arrowianus*, but also contained ***O. maiyasanus*** (subsp. *maiwasanus*, *hokurikuensis*, *suzukanus* and *takiharensis*), ***O. uenoi*** and some individuals of *O. insulicola* and *O. yaconinus* most probably of hybrid origin.

The cluster II (*maiwasanus*-lineage) contained exclusively *O. maiwasanus* (mostly subsp. *maiwasanus* and *hokurikuensis*), details of which will be discussed elsewhere.

The composition of the cluster III (Fig. 1 b) was quite heterogeneous, containing ***O. arrowianus murakii***, ***O. maiwasanus*** (subsp. *suzukanus*, *ohkawai*, *maiwasanus*, *takiharensis*, *shigaraki* and *yoroensis*), ***O. iwawakianus*** (subsp. *shima*, *narukawai* and *iwawakianus*), ***O. yaconinus*** (subsp. *sotai*, *cupidicornis* and “*yamaokai*” from Wakayama) and *O. dehaanii*.

The cluster IV (Fig. 1 a) was mostly composed of ***O. iwawakianus kiiensis***. One example morphologically referable to subsp. *muro* was also included in this cluster. Besides, one example of ***O. arrowianus murakii***, some specimens of ***O. maiwasanus*** (subsp. *yoroensis* and *suzukanus*) and a presumable natural hybrid between ***O. maiwasanus*** and ***O. iwawakianus*** were also the components of this cluster. Note that none of the three subspecies of ***O. iwawakianus*** in the cluster III (subsp. *shima*, *narukawai* and *iwawakianus*) were included in this cluster. Also noticeable is that *suzukanus*, one of the subspecies of ***O. maiwasanus***, appeared in both the clusters III and IV.

Phylogenetic tree of the ITS I (Fig. 2)

The ITS I phylogenetic tree of *Ohomopterus* from the Kinki and Chûbu Districts (Fig. 2 a) contained seven major clusters hereafter called A to G. Of these, we discuss mainly on the clusters A, B and F. The minor ITS I heterogeneity due to its existence in the form of multi-copy within the same species, as well as rather small overall sequence differences of the *Ohomopterus* species, made it possible only to separate the major clusters (with the exception of the cluster B; see below), and thus the branching order of the specimens examined within a given cluster was not satisfactorily determined.

The cluster A (Fig. 2 b) contained the subspecies of ***O. iwawakianus*** (subsp. *iwawakianus*, *kiiensis*, *muro*, *narukawai* and *shima*). Also included were all the subspecies of ***O. maiwasanus*** (subsp. *maiwasanus*, *yoroensis*, *suzukanus*, *shigaraki*,

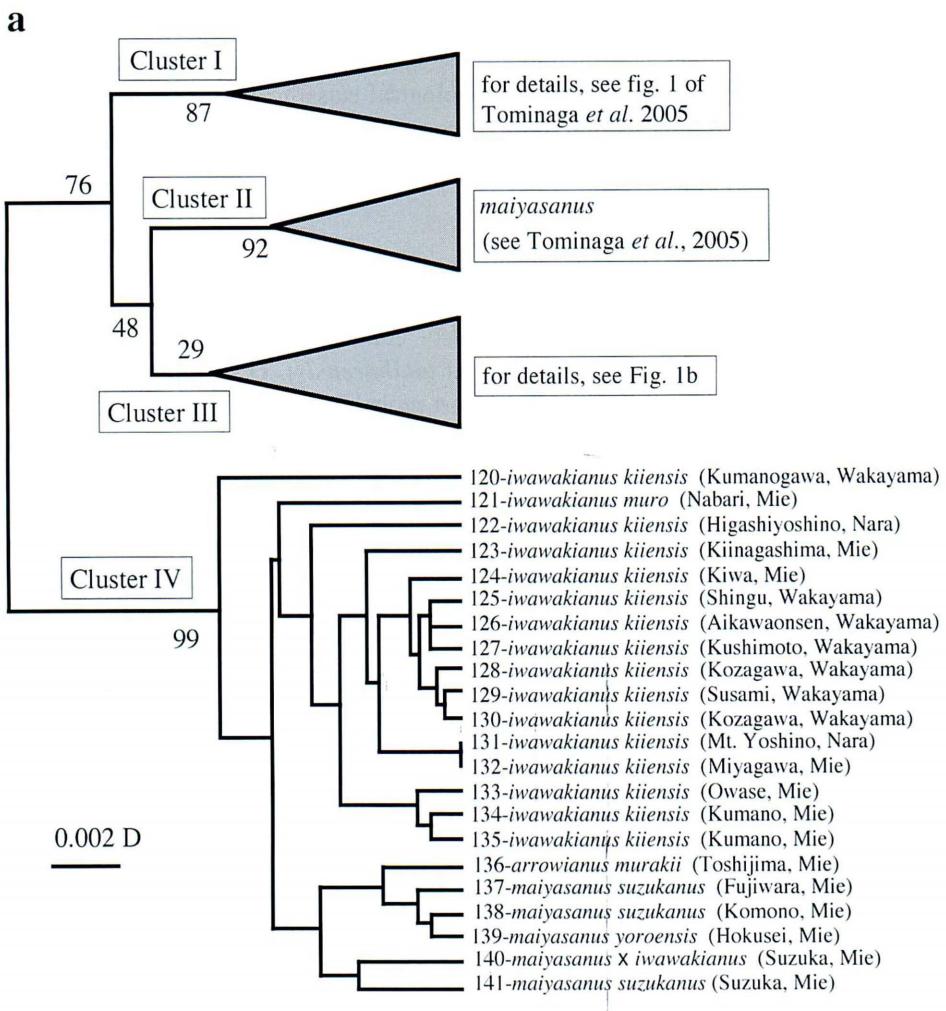
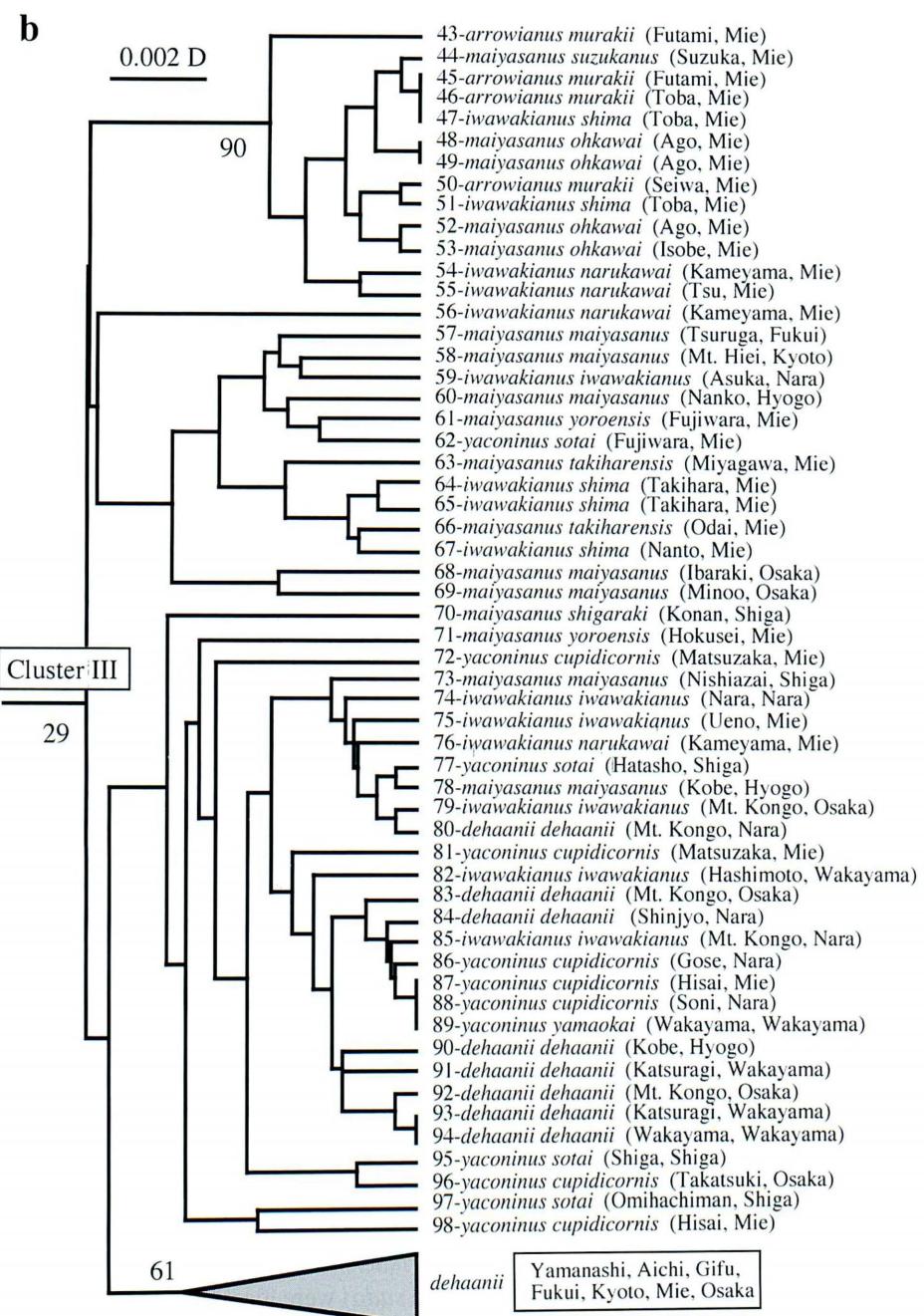


Fig. 1 (on pp. 16–17). UPGMA-phylogenetic tree of the mitochondrial ND5 gene of *Ohomopterus* specimens from the Kinki and Chûbu Districts. — a, General view; b, details of the cluster III

ohkawai, *takiharensis* and *hokurikuensis*), *O. uenoi*, some specimens of *O. arrowianus* (subsp. *minoensis* and *murakii*) and the two subspecies of *O. yaconinus* (subsp. *cupidicornis* and *sotai*). Note that all the subspecies of *O. iwawakianus* including subsp. *kiensis* and *muro* appeared in this cluster. The ND5 gene from *kiensis* and *muro* belongs to the cluster IV, in contrast to that of the remaining three subspecies (nominotypical *iwawakianus*, *shima* and *narukawai*) which belong to the cluster III.

The cluster B (see TOMINAGA *et al.*, 2005, fig. 2 a**) included several subspecies

**) Some subspecific names used in this paragraph are not shown in fig. 2 a of TOMINAGA *et al.* (2005).



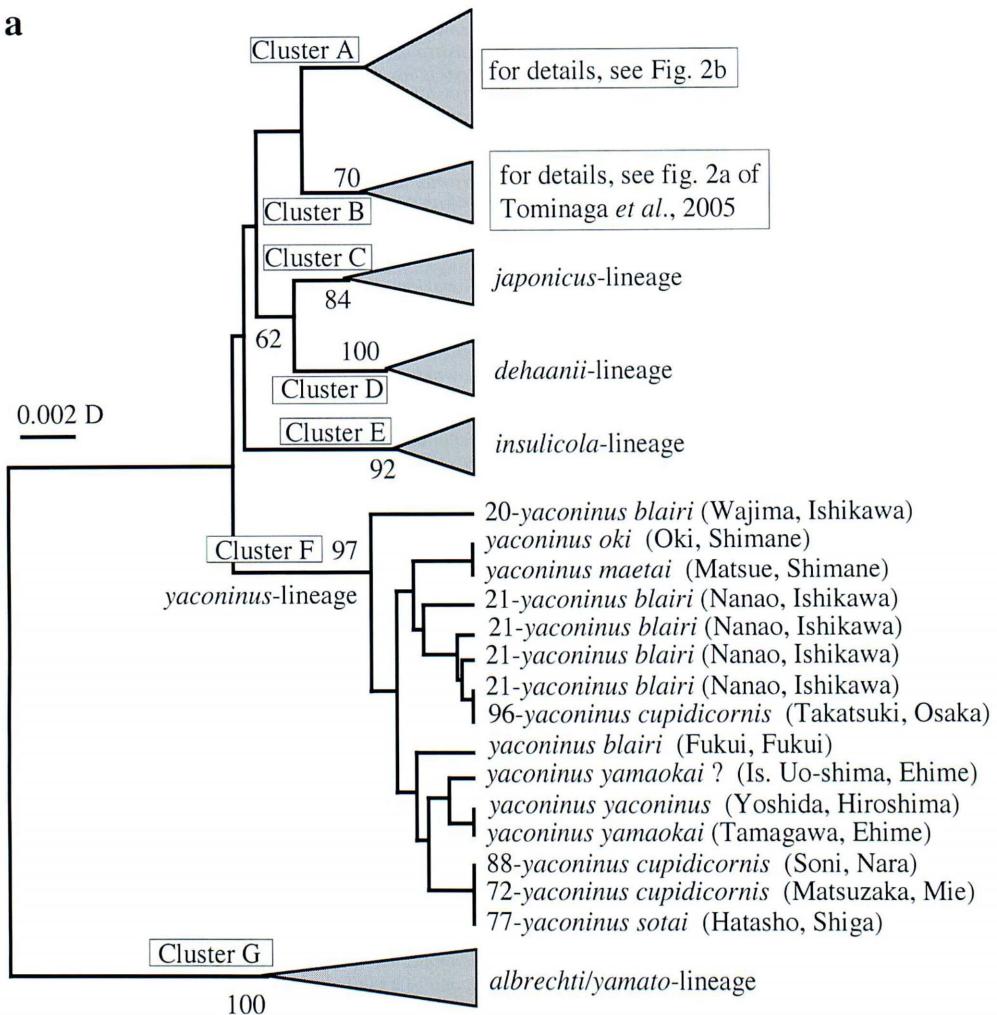
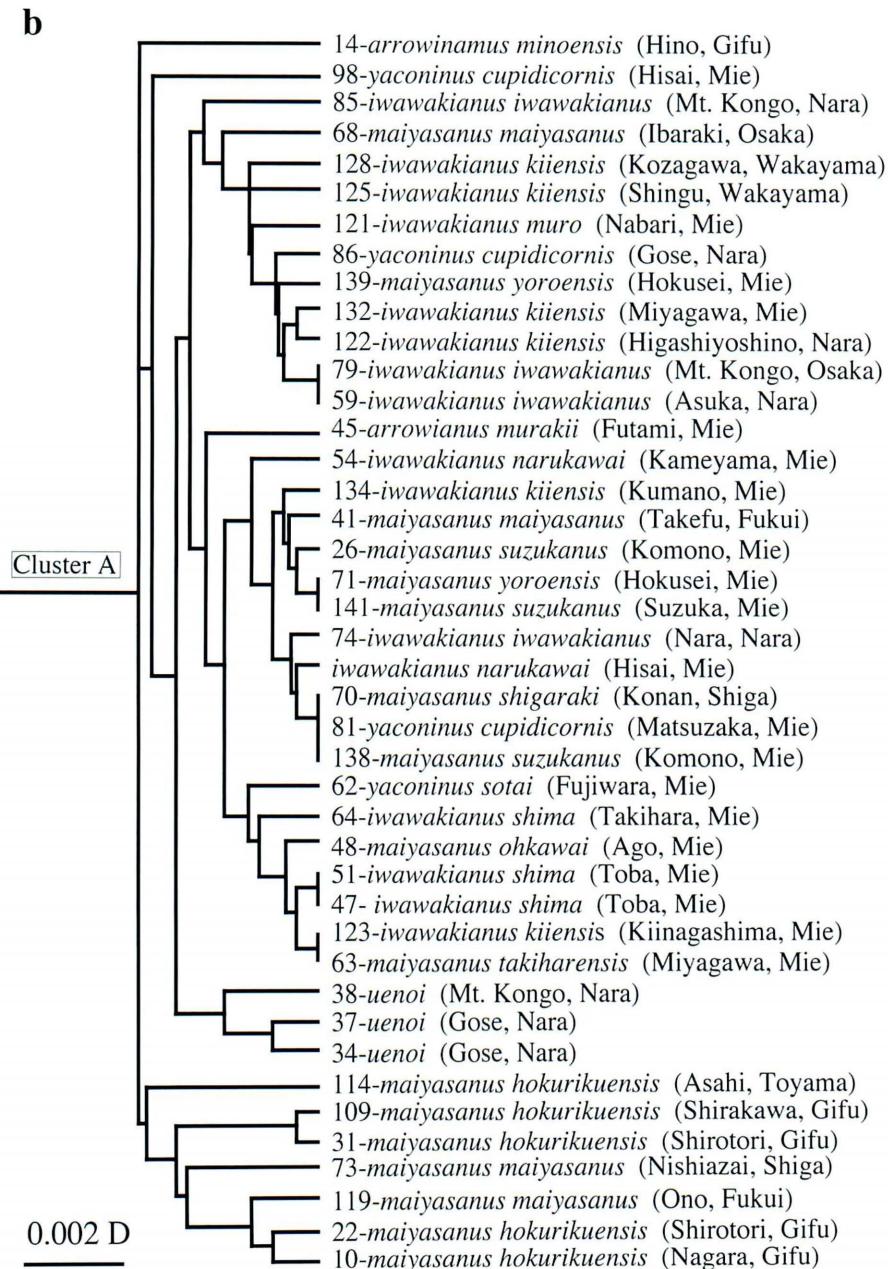


Fig. 2 (on pp. 18–19). UPGMA-phylogenetic tree of the nuclear ITS I sequence of *Ohomopterus* specimens from the Kinki and Chubu Districts. The number before the scientific name corresponds to that of Fig. 1. Some specimens without the number represent the lack of the ND5 sequences. — a, General view; b, details of the cluster A.

of *O. arrowianus* (subsp. *komyai*, *murakii*, *nakamurae*, *kirimurai*, *minoensis* and *arrowianus*) and *O. maiyasanus* (subsp. *hokurikuensis* and *maiyasanus*). Some examples of *O. insulicola* (subsp. *shinano*, *kiso* and *sado*) were also included here, but they are considered to be of the hybrid origin between *O. arrowianus* and *O. insulicola*. Most of the subspecies of *O. maiyasanus* appeared in both the clusters A and B.

The main constituents of the clusters C, D, E and G were *O. japonicus*, *O. de-*



haanii, *O. insulicola* and *O. albrechti/O. yamato*, respectively, and the details of which will be published elsewhere.

The cluster F (Fig. 2 a) was composed exclusively of *O. yaconinus* (subsp. *blairi*, *oki*, *maetai*, *cupidicornis*, *yamaokai*, *yaconinus* and *sotai*).

The molecular phylogeny of the *Ohomopterus* species not dealt with in this paper will be published consecutively.

Discussion

In this section, each cluster of the ND5 and ITS I trees is abbreviated respectively to ND5-I, -II, -III, -IV and ITS-A, -B, -F.

Origin of O. iwawakianus and its subspecies

Of the five subspecies of *O. iwawakianus*, subsp. *kiiensis* is distributed in the greater part of the Kii Peninsula. The specimens from this range have the gene type of ND5-IV and the DNA type of ITS-A. Viewed from such a one to one correspondence of the ND5 gene and ITS I, and also from well defined distributional range without co-existence of any other *Ohomopterus* species in most places, it is strongly suggested that subsp. *kiiensis* represents an authentic strain and it should be regarded as a good species. Though we have examined only a single specimen referable to subsp. *muro* (from Nabari), it shows the same profile as in *kiiensis* in both the ND5 and ITS I trees. On the other hand, three other subspecies (*iwawakianus*, *narukawai* and *shima*) also have the ITS-A type DNA sequence and yet they have the mitochondrial gene type of ND5-III which would have been derived from the female of *O. maiyasanus* (TOMINAGA *et al.*, 2005). Thus, these three subspecies of *O. iwawakianus* would be the descendants of hybrids between the male of *kiiensis* and the female of certain other species, most probably *O. maiyasanus*. They would not represent an authentic strain and it would be problematic to regard them as “subspecies” or “geographical race” in a sense currently used in the taxonomy. The populations represented by these three names are rather sporadically distributed in the area between the range of *kiiensis* and that of *O. maiyasanus*. This fact is consistent with the above view.

Extensive involvement of O. iwawakianus in the subspecific differentiation of O. maiyasanus

Many subspecies of *O. maiyasanus* (see Results and Fig. 2 b) have the DNA type of ITS-A, which all the subspecies of *O. iwawakianus* also have. Distributional ranges of these two species adjoin each other or partly overlap in Mie Prefecture, i.e., *O. m. suzukanus/O. m. yoroensis* and *O. i. narukawai* on and near the Suzuka Mountains, *O. m. takiharensis/O. m. ohkawai* and *O. i. shima* on and near the Shima Peninsula. Their ND5 sequences are variable; they separately appeared mainly in ND5-I, -II and -III. The ND5-I gene was derived mainly from the *arrowianus*-lineage, and that of ND5-II from the *maiwasanus*-lineage. Four specimens of *O. maiyasanus* exceptionally

appeared in ND5-IV (Nos. 137, 138 & 141, subsp. *suzukanus* from northern Mie; No. 139, subsp. *yoroensis* from the Suzuka Mts.), together with a presumable natural hybrid between *O. maiyasanus* and *O. iwawakianus* collected from the hybrid zone of these two species on the eastern slope of the Suzuka Mountains. These four examples are also supposed to be the hybrids with involvement of *O. iwawakianus*. Then, why do they have the combination of ITS-A and ND5-IV, and not of ITS-C and ND5-I or ND5-II which *O. maiyasanus* might have to carry, and why are their male genitalic features of *O. maiyasanus*-type and not of *O. iwawakianus*-type? The most plausible answer is that the female of *O. maiyasanus* first hybridized with the male of *O. iwawakianus* so as to produce a hybrid having the combination of ND5-II and ITS-A, and such a hybrid hybridized again with the male of *O. iwawakianus*. Then, some of the resultant offspring would become to have the combination of ND5-IV and ITS-A. The reason why such a secondary hybrid reveals the morphology of *O. maiyasanus* would be that the ITS I and gene(s) responsible for the species-specific morphologies are separately exist either on the same or different chromosomes, and the inter- or intra-chromosomal chimera formation upon, or some generations after, hybridization would have occurred. Then, there would be a chance for independent inheritance of the ITS I and the genes determining the morphological characters. In the above case, it is possible that the latter gene(s) was introduced to the hybrids independently from the ITS I at a certain stage during the successive hybridizations. Note that *O. iwawakianus* was derived by hybridization between *kiensis* and *O. maiyasanus* and may have the gene(s) determining certain morphological characters of *O. maiyasanus*.

It would be most probable that the populations of *Ohomopterus maiyasanus* belonging to ITS-A and ND5-III (subsp. *maiwasanus*, *shigaraki*, *takiharensis* and *ohkawai*) are also the hybrid-derivatives between the female of certain species in ND5-II and the male of *O. iwawakianus*. The specimens of *O. maiwasanus* belonging to ITS-A and ND5-I (represented mainly by subsp. *maiwasanus* and *hokurikuensis*) are of special interest, because their ND5 genes are not of the *O. maiwasanus*-type but of the *O. arrowianus*-type. The sequence of events would be that the ND5 gene of *O. maiwasanus* was replaced by that of *O. arrowianus* through hybridization of these two species, and the female of their resultant hybrids hybridized again with the male of *O. iwawakianus*.

Other species having the DNA type of ITS-A

Ohomopterus uenoi would most probably be the offspring of a hybrid between the female of *O. arrowianus* and the male of *O. iwawakianus* (TOMINAGA *et al.*, 2005). *Ohomopterus arrowianus murakii* is a hybrid descendant between the male of *O. arrowianus* and the female of certain species having the gene type of ND5-III (to be published elsewhere). In this case, a probable candidate for the female is *O. iwawakianus*, since the female genitalia of *O. a. murakii* is quite similar in shape to those of *O. iwawakianus* as compared with those of the other species in ND5-III. *Ohomopterus arrowianus kirimurai* carries the DNA type of ND5-II and ITS-B, both of which are of

O. arrowianus-type. However, it might be possible that *O. a. kirimurai* is a hybrid-derived chimera between the female of *O. arrowianus* and the male of *O. iwawakianus*, since the female genitalia are of the *O. iwawakianus*-type (IMURA *et al.*, 2005). Of all the specimens of *O. yaconinus* from the Kinki District (subsp. *cupidicornis* and *sotai*), about half the examples had the DNA type of ND5-III and ITS-A, suggesting that they are the hybrid derivatives between the female of an authentic *O. yaconinus* (mainly distributed in the Chûgoku and Shikoku Districts) and the male of *O. iwawakianus*. The remaining half had the combination of ND5-III and ITS-F (see OKAMOTO *et al.*, 2005, on other pages of this volume).

Faunal establishment of O. iwawakianus and the allied taxa in the Kinki District

From what we have discussed above, a scenario for the process of faunal establishment of *O. iwawakianus* and its allied taxa may be deduced as follows.

As noted previously, the population represented by *kiiensis* and probably at least a part of *muro* would be an authentic strain (=good species) distributed in the greater part of the Kii Peninsula, and has been an inhabitant since the Japanese Islands were separated from the eastern periphery of the Eurasian Continent (TOMINAGA *et al.*, 2000). What we now call the nominotypical *iwawakianus*, *shima* and *narukawai* would have become differentiated around the northern periphery of the range of *kiiensis*. This would have occurred through hybridization of the female of *kiiensis* with the male of *O. maiyasanus*. *Ohomopterus maiyasanus* had originally occupied the range along the coastal area of the Sea of Japan in the Kinki and Chûbu Districts, and migrated southwards. Then, *iwawakianus*-*shima*-*narukawai* so formed expanded their range northwards, having reached the Hokuriku District as well as eastwards on and around the Shima Peninsula. The present distributional ranges of *iwawakianus*-*shima*-*narukawai* are rather sporadically recognized adjoining the northeastern periphery of the range of *kiiensis*-*muro*. However, their ranges in the past time were assumed to be much wider than those recognized at present. The populations occurred outside the present distributional ranges of *iwawakianus* would have become extinct for some reasons. This view is supported by the fact that the same DNA of ITS-D can be found in other races inhabiting the above mentioned area, i.e., several subspecies of *O. maiyasanus* and *O. uenoi*. The ND5 gene of most of *O. arrowianus* *murakii* and a part of *O. yaconinus* from the Kinki District has presumably been derived from *O. iwawakianus*. In addition, some specimens of *O. arrowianus* *murakii* or *O. yaconinus* from the Kinki District have the DNA of ITS-F type (neither A nor B). These facts suggest that the female of these two hybridized again with the male of *O. iwawakianus*. Most of the subspecies of *O. maiyasanus* (*maiwasanus* (in part), *hokurikuensis* (in part), *yoroensis*, *suzukanus*, *shigaraki*, *takiharensis* and *ohkawai*) would have formed by hybridization between *iwawakianus*-*shima*-*narukawai* and *O. maiyasanus* during the process of migration of the former towards the north or east, suggesting that these morphologically defined “subspecies” of *O. maiyasanus* are nothing but the offspring produced by such hybridizations, and not pure geographical races within an authentic strain.

From the above discussion, it is evident that so-called *O. iwawakianus* has played an important role for the faunal establishment of the genus *Ohomopterus* in the Kinki District.

Acknowledgements

We thank Hideko KANDA for her skillful technical assistance. Thanks are also due to all our colleagues who collaborated with us either by supplying invaluable materials or by providing useful suggestions. This study is supported in part by the Grant-in-aid No. 13575013 for Scientific Research (B) from the Japan Society for the Promotion of Science.

要 約

井村有希・富永 修・柏井伸夫・岡本宗裕・蘇 智慧・秋田勝己・小鹿 亨・大澤省三：ミトコンドリア ND5 遺伝子と核 ITS I DNA の解析からあきらかになったイワワキオサムシの系統的特性：近畿地方のオオオサムシ属相形成過程におけるその広範な関与。——イワワキオサムシとその関連種のミトコンドリア ND5 遺伝子と核 ITS I DNA の塩基配列を決定して分子系統樹を作製し、検討をくわえた。その結果、これまでイワワキオサムシの亜種として扱われてきたキイオサムシ（およびムロウオサムシの少なくとも一部）は純系の独立種として扱うべきであること、そして、イワワキオサムシ基亜種・ヌノビキオサムシ・シマオサムシの3亜種は、キイオサムシとマヤサンオサムシとの交雑に由来する集団であるらしいことが判明し、これまで形態学的に单一の多型種として扱われてきたイワワキオサムシが、近畿地方におけるオオオサムシ属相の形成過程において重要な役割を果たしてきたらしいことが浮き彫りになった。

References

HIURA, I., 1965. Distribution of *Apotomopterus* beetles in the Kongô-Ikoma Mountain Range, central Kinki, Japan, with special reference to their geohistoric backgrounds (Coleoptera: Carabidae). *Bull. Osaka. Mus. nat. Hist., Osaka*, (18): 49–68. (In Japanese, with English title and summary.)

IMURA, 2002. Classification of the subtribe Carabina (Coleoptera, Carabidae) based on molecular phylogeny. *Elytra, Tokyo*, **30**: 1–28.

—, K. AKITA, M. OKAMOTO, O. TOMINAGA, N. KASHIWAI, Z.-H. SU, T. OJIKI & S. OSAWA, 2005. On *Ohomopterus arrowianus kirimurai* (Coleoptera, Carabidae) as examined by phylogenetic trees of mitochondrial ND5 gene and nuclear ITS I DNA as well as morphology of genital organs. *Ent. Rev. Japan, Osaka*, **60**: 35–38.

— & K. MIZUSAWA, 1996. The *Carabus* of the World. In FUJITA, H. (ed.), *Mushi-sha's Iconographical Series of Insects*, 2. 261 pp., 84 pls. Mushi-sha, Tokyo. (In Japanese, with English book title and summary.)

ISHIKAWA, R., 1985. Carabidae (Carabinae). In UÉNO, S.-I., Y. KUROSAWA & M. SATÔ (eds.), *The Coleoptera of Japan in Color*, **2**: 54–88. Hoikusha, Osaka. (In Japanese, with English book title.)

— & K. KUBOTA, 1996. Geographic races of *Carabus iwawakianus* (NAKANE) in Honshu, Japan: a tentative revision (Coleoptera, Carabidae). *Bull. biogeogr. Soc. Japan, Tokyo*, **50**: 39–50.

KAMIYOSHI, M., 1963. On the female genitalia of *Apotomopterus* from Japan (Col. Carabidae). *Ins. Sci.*,

Osaka, (13): 1–7. (In Japanese, with English title.)

KATSURA, K., O. TOMINAGA, I. HIURA, N. DOI, K. HARUSAWA & K. TANI, 1978. Distribution of carabid beetles in the Ise–Shima region, Kinki District, with description of a new subspecies. *Bull. Osaka Mus. nat. Hist., Osaka*, (31): 47–60. (In Japanese, with English title, summary and description.)

Kinki Research Group of Carabid Beetles (TOMINAGA, O., K. KATSURA, K. HARUSAWA, I. HIURA, K. TANI & N. DOI), 1979. Carabid beetles of the Kinki District in the collection of the Osaka Museum of Natural History. *Spec. Publ. Osaka Mus. nat. Hist., Osaka*, 83 pp. (In Japanese, with English book title.)

NAKANE, T., 1953. New or little known Coleoptera from Japan and its adjacent regions. — IX. Caraboidea II.—. *Scient. Rept. Saikyo Univ., Kyoto*, (Nat. Sci. & Liv. Sci.), **1**: 93–102.

OKAMOTO, M., O. TOMINAGA, Z.-H. SU, Y. IMURA, N. KASHIWAI, T. OJIKI, K. AKITA & S. OSAWA, 2005. Differentiation of *Ohomopterus yaconinus* and its “subspecies” (Coleoptera, Carabidae) inferred from DNA sequences of mitochondrial ND5 gene and internal transcribed spacer I (ITS I). *Elytra, Tokyo*, **33**: 363–370.

OSAWA, S., Z.-H. SU & Y. IMURA, 2004. Molecular Phylogeny and Evolution of Carabid Ground Beetles. 191 pp., 119 figs. Springer-Verlag, Tokyo.

SU, Z.-H., O. TOMINAGA, T. OHAMA, E. KAJIWARA, R. ISHIKAWA, T. S. OKADA, K. NAKAMURA & S. OSAWA, 1996. Parallel evolution in radiation of *Ohomopterus* ground beetles inferred from mitochondrial ND5 gene sequences. *J. mol. Evol.*, **43**: 662–671.

TOMINAGA, O., Y. IMURA, M. OKAMOTO, Z.-H. SU, T. OJIKI, N. KASHIWAI & S. OSAWA, 2005. Origin of *Ohomopterus uenoi* (Coleoptera Carabinae: Carabidae) as deduced from comparisons of DNA sequences of mitochondrial ND5 gene and nuclear internal transcribed spacer I (ITS I) with morphological characters. *Ent. Rev. Japan, Osaka*, **60**: 23–33.

_____, Z.-H. SU, C.-G. KIM, M. OKAMOTO, Y. IMURA & S. OSAWA, 2000. Formation of the Japanese Carabina fauna inferred from a phylogenetic tree of mitochondrial ND5 gene sequences (Coleoptera, Carabidae). *J. mol. Evol.*, **50**: 541–549.